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Turtle Mating Systems: Behavior, Sperm Storage, and Genetic Paternity

D. E. Pearse and J. C. Avise

As evidenced by the articles in this volume, a recent increase in interest in the mating systems of poikilothermic vertebrates has focused primarily on fishes, a few amphibians, and squamate reptiles. Turtles by contrast have received relatively little attention, yet they display a wide variety of mating behaviors and life-history characteristics that make them excellent candidates for addressing several aspects of genetic parentage that should contribute to a broader understanding of animal reproductive strategies. Here we focus on genetic studies of the mating systems and reproductive patterns of turtles, specifically with respect to multiple paternity and long-term sperm storage. These phenomena highlight the importance of a temporally extended perspective on patterns of individual reproductive success.

Unlike many birds and mammals, turtles are not known to form pair bonds or cohesive social groups, and neither sex provides parental care beyond nesting (Shine 1988; but see Iverson 1990). A male's contribution to his offspring is therefore limited to fertilization and indirect genetic effects. With respect to a female's choice of mate, any trade-off between social status or territory quality on the one hand, and male genetic quality on the other, is presumably much reduced. Thus instead of asking under what circumstances a female may seek extrapair copulations (as has been done in many bird species; e.g., Double and Cockburn 2000; Kempnaers et al. 1992), questions about turtle mating systems revolve around the number or quality of a female's mates, the timing of her remating decisions, her capacity for sperm storage (Galbraith et al. 1993; Kaufmann 1992), and the fitness ramifications of a long reproductive life (Gibbons 1987). Female turtles are unlikely to receive many of the proposed direct benefits of multiple mating (e.g., parental care, nuptial gifts), so indirect benefits (e.g., genetic contributions) presumably play a more singular role in mate choice and paternity distributions in turtles than has been found in most bird, fish, and mammal species studied (Andersson 1994; Birkhead 1995).

The aims of this review are to discuss aspects of turtle biology relevant to field-based studies of sperm storage and reproduction; review the available literature on

the genetic mating systems of turtles; consider hypotheses for the evolutionary benefits of multiple mating and sperm storage in this taxon; and highlight future research directions that might take advantage of the unique opportunities afforded by the reproductive biology of turtles. This is not intended to be a comprehensive review of sperm storage and competition, but a focused treatment on the special features of turtles relevant to paternity analysis and mating system studies. For a more comprehensive treatment of sperm competition in reptiles, see Olsson and Madsen (1998).

Reproductive Biology of Turtles

Social Structure and Behavior

Although turtles typically do not display pair bonds or family group affiliations, social organizations exist in some species. For example, dominance hierarchies have been described in gopher tortoises (*Gopherus agassizii*; McCrae et al. 1981), and individuals of this species as well as snapping turtles (*Chelydra serpentina*) also defend home ranges that may be important in mate access or control (Galbraith et al. 1987, 1993; McCrae et al. 1981). Home ranges may not be exclusively guarded, but males occupying overlapping areas often establish dominance through fights (Galbraith et al. 1987; McCrae et al. 1981).

In wood turtles (*Clemmys insculpta*), male dominance hierarchies also exist, and male rank has been shown to affect

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Table 1. Summary of molecular genetic studies of paternity in freshwater and marine turtles

Species	Habitat	Technique	No. of clutches assayed	No. of hatchlings sampled per clutch (n or \bar{n}) ^a	Clutches with multiple paternity (%)	Sperm storage?	Reference
Snapping turtle (<i>Chelydra serpentina</i>)	Freshwater	DNA fingerprinting	3	$\bar{n} = 12$	66	Not assayed	Galbraith et al. 1993
Wood turtle (<i>Clemmys insculpta</i>)	Freshwater	DNA fingerprinting	10	—	50	Not assayed	Galbraith 1991
Painted turtle (<i>Chrysemys picta</i>)	Freshwater	Microsatellites (3 polymorphic loci)	113	$\bar{n} = 5.5$	13	Yes, within season and across years	Pearse et al., in press
Painted turtle	Freshwater	Microsatellites (3 polymorphic loci)	23	$\bar{n} = 7.4$	4	Not assayed	McTaggart 2000
Side-neck turtle (<i>Podocnemis expansa</i>)	Freshwater	Microsatellites (8 polymorphic loci)	2	$\bar{n} = 33$	100	Not assayed	Valenzuela 2000
Leatherback turtle (<i>Dermochelys coriacea</i>)	Marine	Microsatellites (6 polymorphic loci)	17	$\bar{n} = 10$	0	Yes, within season	Dutton et al. 2000
Leatherback turtle	Marine	Microsatellites (2 polymorphic loci)	4	—	0	Not assayed	Rieder et al. 1998
Loggerhead turtle (<i>Caretta caretta</i>)	Marine	Microsatellites (2 polymorphic loci)	3	$\bar{n} = 21$	33	Not assayed	Bollmer et al. 1999
Loggerhead turtle	Marine	Allozymes (4 polymorphic loci)	45	$\bar{n} = 21$	29	Yes, within season	Harry and Briscoe 1988
Loggerhead turtle	Marine	Microsatellites (2 polymorphic loci)	38	$\bar{n} = 10$	21	Not assayed	Moore and Ball 2000
Green turtle (<i>Chelonia mydas</i>)	Marine	Microsatellites (5 polymorphic loci)	22	$\bar{n} = 22-58$	9	Yes, within season	Fitzsimmons 1998
Green turtle	Marine	DNA fingerprinting	3	$\bar{n} = 10.7$	33	Not assayed	Parker et al. 1996
Kemp's ridley turtle (<i>Lepidochelys kempi</i>)	Marine	Microsatellites (3 polymorphic loci)	26	$\bar{n} = 1-14$	58	Yes, within season	Kichler et al. 1999
Desert tortoise (<i>Gopherus agassizii</i>)	Terrestrial	Allozymes (3 polymorphic loci)	12	$\bar{n} = 5$	50	Yes, >2 years	Palmer et al. 1998

^a Depending on information given by the authors.

reproductive success. Males who consistently win fights against other (usually smaller) males enjoy a higher dominance rank and greater access to extended copulations with females (Kaufmann 1992). Based on DNA paternity data, high-ranking males were found to father a significantly greater number of offspring than those of lower rank (Galbraith 1991).

Movement and dispersal are other important behaviors that influence a species' mating system in a given population. In some freshwater turtles, gender differences exist in dispersal tendencies or in total distance traveled per year (Morreale et al. 1984). In addition, the two sexes may differ in seasonal activity levels, with females more active in the nesting seasons of late spring or early summer (in north temperate regions), and males more active in the fall (Gibbons 1968; MacCulloch and Secoy 1983; Pearse 1923). These movements have been interpreted as corresponding to peaks in female nesting and male mate-searching activities, respectively (MacCulloch and Secoy 1983).

Marine turtles present an entirely different life history, with intervals of several years between breeding events, and long distances traveled between communal feeding and nesting grounds (Kuchling 1999; Limpus et al. 1994). Little is known about the behaviors of marine turtles at

sea, but both male and female green turtles (*Chelonia mydas*) have been observed mating more than once over a several-day period, immediately prior to the nesting season (Booth and Peters 1972). Such multiple mating raises questions about mate choice, sperm competition, and genetic paternity of the offspring. Thus, as has also been found for some lizards (Bull et al. 1998), social aspects of turtle biology may prove more important than previously thought for mating system patterns.

Morphology of Sperm Storage Organs

An important aspect of turtle reproductive biology is the ability of females to store viable sperm in their oviducts for long periods of time (Gist and Jones 1989). Females of many other taxa have evolved this ability as well (Birkhead and Møller 1993). In many social insects, for example, a queen mates prior to entering the nest and then uses only this initial sperm to fertilize eggs throughout her reproductive lifetime, which may last for years and involve the production of thousands or millions of progeny (Fjerdingstad and Boomsma 1998; Page 1986). Among the vertebrates, turtles and snakes can store sperm for by far the longest periods. In species representing these two groups, reports exist of a female's continued offspring production for up to 4 and 7 years,

respectively, following isolation from males (Ewing 1943; Magnusson 1979) (although the possibility of parthenogenesis was not eliminated).

Sperm storage tubules in turtles are located in the posterior portion of the albumin-secreting region of the oviduct, a position different from that of other vertebrates (Gist and Jones 1989). The widespread occurrence of such tubules in the Testudines suggests that sperm storage, either between mating and ovulation or over longer time periods (see beyond), is an important component of turtle reproductive biology (Gist and Jones 1989).

Genetic Studies of Paternity

Molecular Documentation of Multiple Paternity

To date, only a handful of surveys have examined genetic paternity in turtle broods from nature, but virtually every study has documented multiple paternity, typically in a high percentage of clutches (Table 1). Few of these genetic analyses entailed large numbers of clutches or incorporated behavioral or ecological data, but they nonetheless amply confirm that multiple paternity is a common phenomenon in both marine and freshwater turtle species. In some cases, more than one study has examined the same species, and

the differences and similarities between their estimates are especially informative.

Concerning marine species, Harry and Briscoe (1988), in allozyme assays, documented multiple paternity in about one-third of the loggerhead turtle clutches assayed. Two later studies examined paternity in loggerheads using microsatellites and found similar (Bollmer et al. 1999) or slightly lower (Moore and Ball 2000) estimates of multiple paternity. Multiple paternity was conclusively documented in nearly 60% of the clutches in the Kemp's ridley population (*Lepidochelys kempi*; Kichler et al. 1999), although a maximum-likelihood estimator suggested the actual value to be closer to 100%. Parker et al. (1996) showed that a large proportion of clutches of the green turtle (*Chelonia mydas*) also can be multiply sired (Table 1). However, a high frequency of multiple paternity has not invariably been found in genetic assessments of sea turtle populations, even in the same species. Fitzsimmons (1998) detected multiple paternity in less than 10% of 22 green turtle clutches, and this was attributable to additional sires for only 3 of more than 900 hatchlings assayed. This genetic finding was surprising given the behavioral observations of promiscuous mating by green turtle females prior to the nesting season (Booth and Peters 1972). Similarly, two studies of leatherback turtles have also found females to be surprisingly chaste; indeed, this is the only species of turtle in which multiple paternity has not been observed (Dutton et al. 2000; Rieder et al. 1998; but see Curtis et al. 2000).

In freshwater turtles also, multiple paternity has been found in every species examined, including wood turtles, snapping turtles, giant Amazon sideneck turtles, and painted turtles (Table 1). In most cases, a high proportion of the clutches examined showed evidence of multiple paternity. All of these studies demonstrate that female turtles in nature may mate with more than one male and that these copulations often result in multiple sires of a clutch.

Sperm Storage by Females

Studies discussed in the previous section have demonstrated that sperm from multiple males are often present in a female's reproductive tract simultaneously, and that these stored sperm can result in multiple sires within a clutch. Sperm storage raises the possibility that a female might be able to influence the paternity of her clutch at the time of fertilization rather

than through her mating choices alone. For a female, sperm storage has another potential consequence—in principle, it allows her to mate on average with less than one male per clutch. A female who mated with a high-quality male, for example, might choose not to remate the following year, but instead to use that male's sperm to fertilize additional eggs in a second nesting season. If frequent mating is costly to females (Andersson 1994; Conner and Crews 1980), a reticent mating behavior might enable a female to increase her net genetic fitness by copulating only as often as necessary to fertilize her eggs.

The utilization of stored sperm by female turtles may be addressed both within and across nesting seasons. Temperate freshwater turtles often lay two to four clutches in a summer, depending on the latitude and local conditions. Because of the short interval between nesting bouts (a few days) and the timing of within-season reovulation following oviposition, female turtles are thought not to remate during these internest intervals within a season (Gist and Congdon 1998). If so, sperm storage is necessary for fertilization success in later clutches. Paternity data on successive single-female clutches within a season have supported this hypothesis: For the three turtle species genetically surveyed in this regard, in each case the same male (or set of males) fertilized all of the eggs in successive clutches laid by a given female within a single nesting season (Fitzsimmons 1998; Kichler et al. 1999; Pearse et al., in press).

In captivity, multiyear sperm storage by females is well established, because female turtles isolated from males can continue to produce offspring over time (Ewing 1943; Olsson and Madsen 1998). To determine if females utilize stored sperm despite the option of remating, Palmer et al. (1998) confined female desert tortoises with three males for two breeding seasons and assessed the paternity of their offspring using allozymes. Progeny in 5 of the 12 assayed clutches could not have resulted from pairings of the known mothers with any of the captive males. Thus these offspring were considered to have arisen from fertilizations by sperm stored from previous matings.

The extent to which female turtles in nature utilize sperm stored across years has only recently been examined (Pearse et al., in press). In our genetic paternity analysis of a free-living population of painted turtles on the Mississippi River, more than 20% of the 32 females assayed were doc-

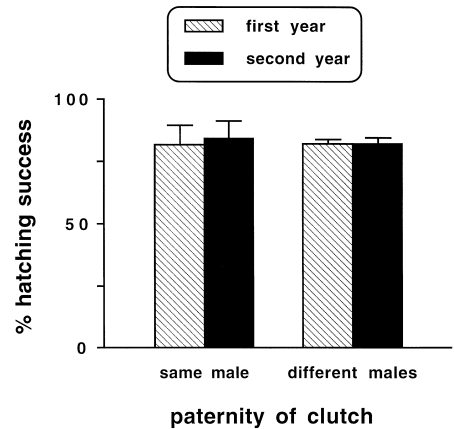


Figure 1. Mean hatching success for pairs of clutches from individual female painted turtles who utilized sperm from the same male or from different males in successive nesting seasons (after Pearse et al., in press). For females who used a single male's sperm, hatching success in the second year is the same or greater than in the first year, suggesting that there is no effective loss in sperm viability.

umented to have used only one male's sperm each for at least two and in one case three consecutive years. This species is noted for its gregarious behavior, so it seems doubtful that females were mate limited (as has been suggested for more solitary species where suitable mates might be infrequently encountered; Connor and Crews 1980; Jun-Yi 1982; see beyond). This sperm storage came at no apparent fitness cost to the females, because clutches fertilized by stored sperm both within and across years had the same hatching success rate as clutches fathered by newly acquired sperm (Figure 1). Moreover, an additional 20% of the females examined used some stored sperm to fertilize clutches in two consecutive years, but also remated between years, resulting in mixed-paternity clutches in the second year (Table 3 in Pearse et al., in press).

For either the within- or across-year cases, sperm storage by females puts strong selective pressure on males to produce sperm that can survive long-term storage. Any such male stands to gain enormous fitness benefits by siring multiple clutches without further reproductive expenditure (Oring et al. 1992).

Evolution of Female Multiple Mating and Sperm Storage

Female Benefits of Multiple Paternity

In general, possible benefits to a female of multiple matings include nuptial gifts, parental assistance from more than one male, and increased genetic diversity among offspring (Andersson 1994). Of

these, only genetic effects on offspring fitness are likely to apply substantially to female turtles. This situation differs from that of many female birds, who must consider social as well as genetic factors when choosing among primary mates who may differ in factors such as quality of territory or transferable resources (Double and Cockburn 2000). Thus perhaps the criteria for mate choice in turtles may be more analogous to a female bird's choice of extrapair partners rather than of primary mates.

Genetic benefits of multiple mating for females turtles are probably important, however, and the almost universal finding of multiple paternity in Chelonian species is consistent with this idea (Galbraith et al. 1993; Harry and Briscoe 1988). The most obvious genetic benefit of mating is egg fertilization, and multiple mating provides a female with insurance against the possibility that one of her mates is less than fully fertile (Olsson et al. 1996). However, insufficient data are available for any turtle species to draw conclusions regarding variation in sperm viability among males, or what the importance of this might be vis-à-vis other selective factors that might behoove females to mate multiple times.

Multiple mating may also increase a female's fitness by encouraging sperm competition and thereby increasing offspring quality (Keller and Reeve 1995; Madsen et al. 1992). This hypothesis was downplayed by Curtsinger (1991), however, who argued that only under very restrictive conditions, including no costs associated with multiple mating, could sperm competition be strong enough to promote the evolution of multiple mating by females.

In painted turtles, preliminary data in an ongoing analysis detected a small but significantly higher rate of hatching success in clutches with multiple paternity (Figure 2; Pearse DE, et al., unpublished data). This difference may have resulted from higher sperm counts due to multiple copulations, or in theory it may have been a consequence of variation among males in genetic compatibility with a given female. In general, such genetic incompatibilities may block egg development, perhaps for reasons that have more to do with interactions between the male and female genomes than with whether males contribute universally "good" or "bad" genes (Kempnaers et al. 1999; Newcomer et al. 1999; Zeh and Zeh 1996). However, in another study of painted turtles, McTaggart

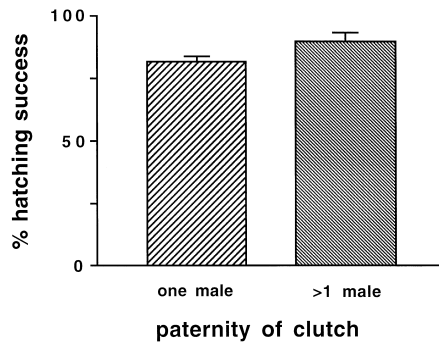


Figure 2. Mean hatching success in individual painted turtle clutches with single versus multiple paternity. The mean hatching success is significantly higher for clutches with multiple paternity (one-tailed t test, $t = -1.94$, $P = .032$), and the variance in hatching success across multiple-paternity clutches is significantly lower (F test for variances, $F = 2.77$, $P = .021$).

(2000) found extremely low levels of multiple paternity, but showed that clutches sired by males who mated successfully with multiple females had significantly higher hatching success. This finding is compatible with the good-genes hypothesis in the sense that mate choice preferences were consistent among females, and that mate choice had an effect on female fitness.

Any of the above-mentioned potential benefits of multiple paternity would only be increased by the ability to store sperm. All else being equal, the longer the time period over which a female stores sperm, the greater the likelihood that she will remate and bring sperm from two or more males into contact. Thus females who store sperm have an increased chance of producing clutches with multiple sires, in which offspring are sired under conditions of sperm competition or cryptic female choice.

Why Store Sperm?

Several selective agents have been proposed for the evolution of female sperm storage organs and the ability to store sperm in reptiles. One is simply to ensure fertilization of future eggs (Connor and Crews 1980; Jun-Yi 1982). This hypothesis predicts that solitary more so than social or abundant species might have evolved enhanced sperm storage capabilities, and Birkhead and Møller (1993) cite chameleon lizards as an example. This prediction does not always hold, however, because sperm storage has been demonstrated in some densely aggregating species, and in any case mate limitation is unlikely to be a problem for any but the most dispersed and least motile of species.

Because of the large egg size in turtles

and distention of the oviduct during oviposition, a potential problem for females is that sperm retained in the oviduct might be pushed out by descending eggs, leaving few sperm to fertilize subsequent clutches (Bakst 1978; Hattan and Gist 1975). Considering this problem, Gist and Congdon (1998) suggested that "the primary function of sperm retention is to provide a supply of gametes to fertilize second and subsequent egg clutches." These authors went on to speculate that females may use recently acquired sperm (still in the oviduct) to fertilize early clutches, but mobilize sperm stored in the ancillary tubules to fertilize later clutches. This prediction was borne out by recent genetic data in painted turtles showing that for each of two females with appropriate clutches, stored sperm had fertilized a portion of the second clutch, whereas the first clutch was fertilized entirely by newly acquired sperm (Pearse et al., in press).

Another explanation for sperm storage relates to the fact that the phenomenon separates the act of copulation from fertilization or egg laying (Birkhead and Møller 1993). If the reproductive cycles of male and female turtles are asynchronous for whatever reason, then sperm storage can serve in effect to appropriately synchronize copulation, fertilization, and nesting. Egg laying in most temperate turtle species occurs in the early summer, and mating activity generally has been thought to peak in spring (Krawchuk and Brooks 1998). However, evidence for male mate searching and spermatogenesis in the fall (Gibbons 1968) suggests that mating activity can occur in that season also, and that over-winter sperm storage may be an important component of the reproductive cycle of some turtle species (see also Thomas et al. 1999). Further evidence for a fall mating period comes from observations of elevated sperm production by males and the presence of sperm in the reproductive tracts of females captured at that time (Gist et al. 1990).

In other vertebrate taxa, effective synchronization of reproductive events is accomplished by delayed implantation (in some mammals), delayed embryonic development, or sperm storage (Birkhead and Møller 1993). The widespread occurrence of such mechanisms led these authors to suggest that considerations of reproductive timing are paramount and hence as phrased by Olsson and Madsen (1998), that the primary function of sperm storage "is not for long term production of clutches from a single mating." None-

theless, recent genetic data document that at least some female turtles employ stored sperm to fertilize multiple clutches within and across years (Palmer et al. 1998; Pearse et al., in press).

Sperm storage could also function as an additional period of mate choice if a female can detect information about male quality from seminal fluids (Eberhard 1998). Such information might come from chemical cues signifying genetic relatedness to the male, or major histocompatibility complex (MHC) similarity, for example, and the female may then select sperm accordingly to fertilize her eggs (Olsson et al. 1996; Peacock and Smith 1997; Potts and Wakeland 1993, but see Cunningham and Cheng 1999). Alternatively female turtles may use information on sperm quality to adjust their investment in resulting offspring. In some bird species, female investment in terms of egg size (Cunningham and Russell 2000) or testosterone level (Gil et al. 1999) has been shown to correlate with mate attractiveness based on phenotypic variation. Other birds are capable of facultative adjustment of offspring sex ratio in response to cues about mate quality (Oddie 1998), as was found in female blue tits (*Parus caeruleus*; Svensson and Nilsson 1996): females mated to males with high "survival quality" skewed their offspring sex ratios toward sons, presumably because such mates might tend to produce high-quality sons. Female turtles have a ready means of adjusting the sex ratio through temperature-dependent sex determination (Janzen 1994), but their use of it in relation to mate quality has not been examined.

Summary and Future Directions

Several novel perspectives on genetic mating systems have come from recent molecular studies on turtles. For example, new light has been shed on the evolution of long-term sperm storage and utilization in nature, female motives for multiple paternity in the absence of strong pair bonds or social interactions, and the genetic consequences of a long reproductive life. With regard to the latter, a female turtle who mates every 3 years with a new male and lays eggs fertilized only by him for several nesting seasons with no multiple paternity could during her lifetime still produce offspring with a total genetic diversity comparable to that of a short-lived bird or mammal with far more promiscuous behavior.

As descriptive studies of turtle mating

systems accumulate, a greater focus is needed on the patterns of utilization of stored sperm, including the effects of mating order and sperm precedence on paternity distributions, and the possibility of active female choice. For example, future work on turtles could examine the conditions under which females choose to store sperm rather than remate. Studies on turtle mating systems would also benefit from data on the male side of the reproductive equation. Little is known about the factors that influence a males' success in sperm competition, sexual selection, or the distribution of reproductive success across individuals. Such information will be important for understanding the evolution of mating systems in turtles and other long-lived species with delayed fertilization and long-term sperm storage mechanisms.

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